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Nursery areas and recruitment variation of Northeast Atlantic mackerel (*Scomber scombrus*)

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There are currently no dedicated recruitment survey data available in support of the assessment of the abundance and distribution of Northeast Atlantic (NEA) mackerel (*Scomber scombrus*), one of the most widespread and commercially important fish stocks in the North Atlantic. This is despite the fact that an estimate of recruitment is an important requirement for the provision of advice to fishery managers. The work here addresses this by compiling catch rates of juvenile mackerel from bottom-trawl surveys conducted between October and March during 1998–2012 and applying a log Gaussian Cox (LGC) process geostatistical model incorporating spatio-temporal correlations. A statistically significant correlation between the modelled catch rates in adjacent quarters 4 and 1 (Q4 and Q1) demonstrates that bottom-trawl surveys in winter are an appropriate platform for sampling juvenile mackerel, and that the LCG model is successful in extracting a population abundance signal from the data. In this regard, the model performed appreciably better than a more commonly used raising algorithm based on survey swept-area estimates. Therefore, the LCG model was expanded to include data from the entire survey time-series, and a recruitment index was developed for use in the annual ICES stock assessment. We hypothesize that catchability is positively density-dependant and provides supporting evidence from acoustic observations. Various density-dependant transformations of the modelled catch rates were furthermore found to improve the correlation between the derived annual recruitment index and recruitment estimated by backcalculation of adult mackerel data. Square root transformation led to the strongest correlation, so this is recommended for further analysis of mackerel abundance. Finally, we provide maps of spatial distributions, showing that the most important nursery areas are around Ireland, north and west of Scotland, in the northern North Sea north of 59°N and, to some extent, also in the Bay of Biscay.

Keywords: acoustic, Cantabrian Sea, catchability, demersal trawl survey, forecast, geostatistics, LGC, mackerel, Northeast Atlantic, North Sea, recruitment, *Scomber scombrus*, stock assessment.

Introduction

Northeast Atlantic (NEA) mackerel (*Scomber scombrus*) is one of the most abundant and widely distributed migratory fish species in the Atlantic (ICES, 2011; Trenkel *et al.*, 2014). It is a purely pelagic species, with spawning areas from the Gulf of Cadiz and into the Mediterranean in the south, to the Faroe Islands in the north, and from south of Iceland in the west to Kattegat in the east. Juvenile mackerel have been observed over a wide area from south of Iceland in the west (Astthorsson *et al.*, 2012; ICES, 2013a) to the Baltic Sea in the east (Alander, 1948; Hamre, 1980) and from the Norwegian North Cape (Lockwood, 1988) to the Iberian Peninsula and Mediterranean Sea in the south. ICES currently assess the mackerel in the North Atlantic as a single stock.

Estimation of recruitment in an exploited fish stock such as mackerel is important both for the general understanding of the dynamics of stock productivity and for the provision of advice to management bodies. For NEA mackerel, there is currently no such recruitment index available, largely because juvenile mackerel are insufficiently represented in the currently available datasets, namely the commercial catch data, the triennial egg survey, and the tagging survey (ICES, 2014a).

Historically, an index of recruitment was obtained from bottom-trawl surveys carried out across the western European shelf from Scotland to Spain. This index was discontinued for short-term predictions in 1995 (ICES, 1995), because perceived trends in the recruitment index were not reflected in the assessment time-series. Given that an estimate of recruitment is a requirement for any short- or medium-term prediction, the survey index was replaced by a long-term (geometric) mean value based on recruitment as calculated by the stock assessment model. More recently, the use of calibration regression to provide an estimate of predicted year-class strength was investigated (ICES, 2008a, b). This methodology was applied to multiple time-series of recruitment indices derived from bottom-trawl surveys. The conclusion of that exercise was that calibration regression might not, at the time, provide a better estimate of mackerel recruitment than the geometric mean of the recruitment series estimated by the assessment model.

This study presents the results of a geostatistical modelling approach based on data from bottom-trawl surveys in October–March over the period 1998–2012, with the aim of producing a time-series of a relative catch-rate index that could be used for assessment, forecast, and provision of advice. Catchability is analysed and accounted for on the basis of acoustic observations, and the resultant juvenile distribution patterns are mapped and described.

Material and methods

Bottom-trawl survey data

A dataset was compiled incorporating observations from bottom-trawl surveys conducted between October and March during 1998–2012 (Table 1). Surveys conducted on the European shelf in the first and fourth quarters are collectively known as the International Bottom Trawl Survey (IBTS). This dataset was supplemented by data from the Faroese bottom-trawl survey, which takes place in the first quarter on the Faroe Plateau and the Icelandic bottom-trawl survey in Q4 and Q1 on the Icelandic shelf. All surveys sample the fish community on the continental shelf and upper shelf slope. IBTS Q4 covers the shelf from Spain to Scotland, excluding the North Sea (Figure 1a), whereas IBTS Q1 covers the shelf waters from north of Ireland, around Scotland, and into the North Sea (Figure 1b). Trawl operations during the IBTS have largely been standardized through the relevant ICES Working Group (ICES, 2013b). Trawling speed was generally 3.5–4.0 knots, and trawl gear is also standardized and collectively known as the Grande Ouverture Verticale (GOV) trawl (Table 1). Some countries use modified trawl gear to suit the particular conditions in the respective survey areas. In some cases, the standard GOV was modified, which was not expected to change catchability significantly. However, subsequent trawls deviated more significantly from the standard GOV type, namely the Spanish BAKA trawl, the Icelandic trawl used in Q1, the French GOV trawl, and the Irish mini-GOV trawl. The BAKA trawl had a vertical opening of only 2.1–2.2 m and was towed at only 3 knots. This was considered substantially less suitable for catching juvenile mackerel and, therefore, was excluded from the analysis. The Icelandic trawl used in Q1 had a vertical opening of only 2–3 m. The French GOV trawl was rigged without a kite and typically had a reduced vertical opening, which may have reduced the catchability of pelagic species like mackerel. A total of 10 intercalibration hauls were available, which were, however, considered too few to calibrate the different variations of the trawl gear used, given the high variance and overdispersion of the catch rates. Catchability was, therefore, assumed to equal the

Table 1. Demersal trawl surveys.

Survey	Quarter	Country	Day of year	Gear	Haul speed (knots)	Wingspread (m)	Vertical opening (m)	From	To
SWC-IBTS	1	SCO	75	GOV	3.7	19.0	4.5	1998	2012
SWC-IBTS	4	SCO	327	GOV	3.7	19.0	5	1998	2012
Faroe Islands	1	FO	70	Box trawl	3.3	18.0	5.0	1998	2012
Iceland	1	ICE	70	Marstroll	3.8	16.8	2–3	1998	2012
Iceland	4	ICE	288	Gulltoppur	3.8	17.0	4–5	1998	2012
Iceland	4	ICE	288	Gulltoppur (66.6 m)	3.8	21.3	5–6	1998	2012
IGFS	4	IRL	311	GOV	4.0	20.6	6[a]	2003	2012
ISCGS	4	IRL	322	Mini-GOV	3.5	8.5	-	1998	2002
EVHOE	4	FRA	308	GOV	3.9	19.0	4[a]	1998	2012
Q4SWIBTS	4	ENG	326	GOV/GOVX	4.0	19.0	4.5	2004	2011
Q1 Spain	1	SP	276	BAKA	4.0	19.0	1.8[a]	1998	2012
Q1 NS IBTS	1	DK/ENG/FRA/GER/NED/NO/SCO/	-	GOV	4.0[a]	20.0	5	1998	2013

Quarter 1 refers to January–March and quarter 4 refers to October–December. Median values are given for day of year, haul speed, wingspread, and vertical net opening.
[a]Source: www.datras.ices.dk.

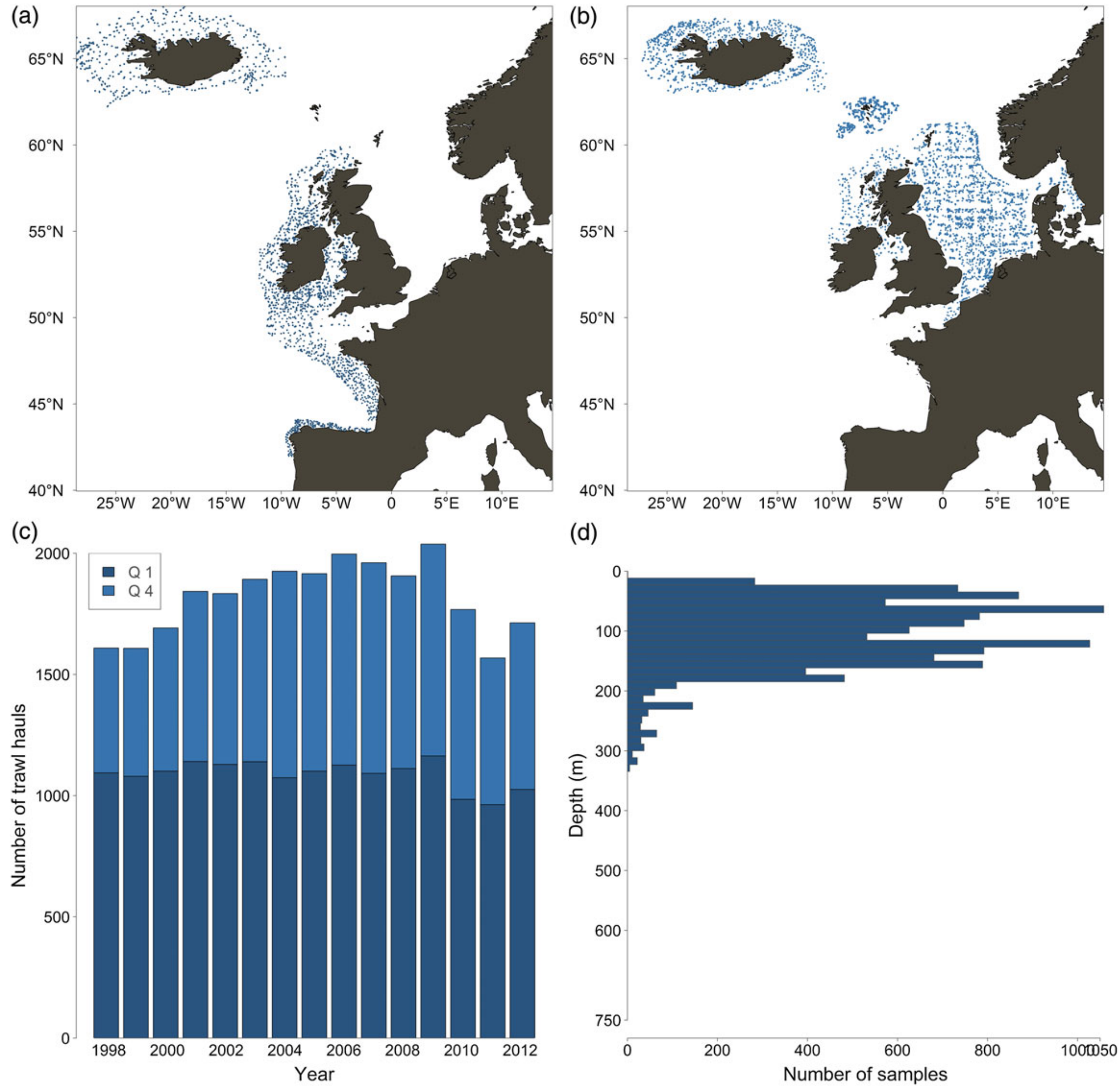

Figure 1. Demersal trawl survey data coverage for 1998 – 2012 in the studied area. (a) Trawl sample locations in the fourth quarter (Q4, October – November, blue dots); (b) trawl sample locations in the first quarter (Q1, January – March, light blue dots); (c) number of samples by year and quarter; and (d) depth.

catchability of the standard GOV trawl, and the associated bias potentially resulting from this assumption was tested in a sensitivity analysis. Finally, the Irish mini-GOV trawl, used during 1998–2002, was a GOV trawl in reduced dimensions. The reduced wing-spread and trawl speed were accounted for in the model (more details below).

Data were downloaded from the ICES repository (http://datras.ices.dk) and supplemented by data from national databases in cases where single surveys had not been submitted to the ICES repository.

The dataset consisted of 27 273 trawl hauls (Figure 1). They were relatively equally distributed over the time-series (Figure 1c); trawling was done during daylight, and most samples were taken on the shelf down to 220 m bottom depth (Figure 1d). The deepest hauls were at 750 m (Figure 1d). Catch in number by length was recorded, and otoliths were subsampled for ageing. A total of 18 300 mackerel were aged from the Irish and Scottish surveys. Catch rates per cm group were converted to catch rate per age group by applying annual age–length keys derived from logistic regression models fitted to all aged mackerel for each year and quarter. Further analysis was restricted to mackerel within their first year of life ("age zero"), i.e. mackerel that, based on their length, would be expected not to have any otolith winter rings (Q4 surveys) or just one winter ring (Q1 surveys).

A total of 31% of the hauls contained mackerel that were <1 year old and equated to a total of 2.0 million mackerel. Catch rates ranged from 0 to 4.6 million mackerel per swept nautical mile^2, with a median of 0 and a mean of 6281.

Geostatistical modelling of catch rates

A geostatistical log Gaussian Cox (LGC) process model incorporating spatio-temporal correlations was used to describe the catch rates of mackerel recruits over space and time.

Related models have previously proved their value for mackerel larvae (Jansen *et al.*, 2012a), cod (*Gadus morhua*) (Lewy and Kristensen, 2009; Kristensen *et al.*, 2013), and whiting (*Merlangius merlangus*) (Nielsen *et al.*, 2014).

In the model formulation used for this study, the response variable was catch in numbers of age 0 mackerel from 15 cohorts (1998–2012). The spatial grid comprised cells of 10 × 10 km. For the Q4 data, this consisted of 966 cells and resulted in 14 490 random variables (1 age class × 15 years × 966 grid cells), which were assumed to follow a log Gaussian distribution that determined the mean of the catch (in numbers), which are assumed to follow a Poisson distribution. This model structure is referred to as an LGC process model and has been shown to be appropriate for count data from catches that are correlated, overdispersed, and zero-inflated (with any 0 values) (Kristensen *et al.*, 2013). The Poisson distribution allows for 0 catches, while the log Gaussian randomness of the density fields imply overdispersed catches (relative to Poisson), both allowing for very high counts and for many more 0 catches than would be found in a pure Poisson model. Furthermore, the catches inherit the correlation structure of the density field.

A key feature of the model was the utilization of information that resides in the patchy distribution of fish, typical for pelagic species. This behaviour was modelled in three parts: large-scale patchiness (correlations between cells) in space and in time as well as local variance between hauls (within a cell), accounting for the tendency of fish to school. The latter was referred to as the "nugget effect".

The large-scale spatial correlation was assumed to decay with distance, and the temporal stability was estimated as the correlation from year to year of the density in a given cell. Both temporal and spatial correlations were assumed to decay exponentially. To avoid correlation over land (e.g. Ireland), the spatial correlation effect is modelled as a Gaussian Markov random field (cell-to-cell chains). The parameter estimates for these correlations are expressed as decorrelation distance (H) and decorrelation time (T), the distance in space and in time where the correlations have decayed to e^{-1} (explaining ca. 14% of the variance). Documentation of these correlation structures were published in Kristensen *et al.* (2013).

The third relation in the model that should reflect fish behaviour was the "nugget effect". Catches of certain fish sizes tend to be overrepresented in trawl hauls compared with the size distribution in the sampled population, likely due to the size-structured nature of schools. This local effect was accounted for by estimating the remaining variation among the hauls with a Gaussian-distributed variance term with a mean of zero (σ_N^2).

Trawling operations largely followed standard IBTS procedures (ICES, 2013a). However, some differences in gear design and operation resulted in variation in the effort (i.e. trawled area). Rather than including the swept area as an offset predictor variable within the model, individual gear parameters [groundspeed (GS), wingspread (WS), and duration (D)] were included. As each parameter can affect the catch in several ways, i.e. when increasing groundspeed, swept area increases, but possibly also catchability because mackerel have to swim faster to avoid the trawl, this was considered appropriate. Increasing tow duration also increases the swept area. Furthermore, this may result in increased catch rates as a result of mackerel swimming in front of the net becoming more fatigued. Conversely, catch rates may be reduced as a result of trawl saturation. In some situations, the trawl was hauled earlier than planned if a large school was caught.

In summary, the expected count of individuals in sample i taken at position x in year y is:

$$E[\log(\lambda_i)] = \eta_{\text{space}}(x) + \eta_{\text{space}\times\text{time}}(x, y) + \mu(y) + \eta_{\text{nugget}}(i) + \mu(GS) + \mu(WS) + \mu(D) \quad (1)$$

where λ_i is the number of 0-year-old mackerel; η_{space} (x) is a mean 0 Gaussian stochastic process with covariance matrix $\exp(-|\Delta x|/H)$, i.e. the "spatial intercept surface"; $\eta_{\text{space}\times\text{time}}$ (x, y) is a mean 0 Gaussian stochastic process with covariance matrix $\exp(-|\Delta x|/H) \times \exp(-|\Delta y|/T)$, i.e. the "space–time surface"; $\mu(y)$ is the year parameter, i.e. a factor with one level for each year; $\eta_{\text{nugget}}(i)$ is mean 0 Gaussian noise with variance (σ_N^2); $\mu(GS)$ is the *groundspeed* parameter; $\mu(WS)$ is the *wingspread* parameter; and $\mu(D)$ is the *duration* parameter.

The parameters in the model were estimated using the maximum likelihood principle based on the Laplace approximation; thus, the estimation follows the principles of Kristensen *et al.* (2013). The final model was used to calculate annual estimates of mackerel catch rates (catch in numbers per swept nautical mile^2) at age 0 in each 10 × 10 km cell.

A catch-rate index could then be derived by integrating the intensity across the spatial surface (sum of catch rates from all cells within a year):

$$I(y) = \int_A \exp[\eta_{\text{space}}(x) + \eta_{\text{space}\times\text{time}}(x, y) + \mu(y)]\, dx \quad (2)$$

where A denotes the spatial area. The best unbiased estimator of $I(y)$ is given by the conditional mean of $I(y)$, given our observations. This is found by simulation:

1. Draw a sample of all latent variables $\eta_{\text{space}}(x) + \eta_{\text{space}\times\text{time}}(x, y) + \mu(y)$ from the posterior distribution given the data.
2. Calculate the index time-series $I(y_1), I(y_2), \ldots, I(y_n)$.
3. Repeat steps 1–2 1000 times.
4. Calculate an annual mean and CV for the simulated indices.

Models were initially fitted separately for Q4 and Q1 surveys. To explore model performance and differences in mackerel catch rates between the two periods, models were fitted to data from the overlap area only and compared.

Catchability

A hypothesis of density-dependent catchability was posed and examined by acoustic observations.

A total of 1073 nautical miles of acoustic survey track collected during the pelagic ecosystem survey in the Western Channel and eastern Celtic Sea (PELTIC) in October 2013 were scrutinized for mackerel schools (ICES, 2014a). Schools were identified by their multifrequency backscatter characteristics (Korneliussen, 2010) in Myriax Echoview, as described in van der Kooij *et al.*, (Submitted). Trawls catches showed a predominant juvenile composition in the area. Each school was characterized as either a bottom or a midwater school according to the distance between the average deepest edge of the school and the bottom. Schools where this distance was <5 m above bottom were categorized as bottom schools; as such, they were likely to be available to gear as deployed on the IBTS. Acoustic observations were limited to daylight to match the IBTS trawling protocols. Acoustic density (NASC, s_A) was used as a proxy for the number of fish. A total of 572 schools were detected, and their densities were compared between the two categories by a two tailed *t*-test.

Alternative indices, adjusted to reduce the density effect, were calculated by transforming the cpue in each cell before calculation of the indices. Square root, cubic root, and log-transformations were applied. Assuming that the relative cohort strengths are preserved until the ages of full selectivity in the fishery and in the International Ecosystem Summer Survey in the Nordic Seas (IESSNS; Nøttestad *et al.*, 2012), the alternative indices can be benchmarked by examining the correlation with two alternative recruit time-series: (i) Assessment I—the recent benchmarked mackerel stock assessment (WKPELA) base run with all input data (modified to exclude the IBTS index) and (ii) Assessment II—the 2013 assessment based on WKPELA methods, updated with the finalized 2013 egg survey results that were unavailable at the time of WKPELA (ICES, 2014a, b). Index comparison was based on r^2.

Cpue from swept area

An alternative raising procedure similar to that used to calculate survey cpue indices in ICES DATRAS and from the IESSNS survey was applied to the IBTS data for comparison with the index described above. The index values were calculated in four steps for each year:

1. Calculation of catch in numbers by swept nautical mile^2 for each trawl station (cpue), from information on haul duration, trawling speed, and wingspread.
2. Calculation of cpue by ICES statistical rectangles (0.5° latitude and 1° longitude). This was calculated as the average cpue of the trawl stations in each rectangle.
3. Cpue in unsampled rectangles was calculated as the average cpue of adjacent sampled rectangles. This was only done for rectangles meeting the following criteria: (i) having been sampled at least once in 1 year and (ii) having samples in a minimum of two of the neighbouring rectangles within the given year.
4. The final index value was calculated as the weighted average of cpue of rectangles, weighted by the sea area. The sea area of each rectangle was calculated using the R packages "geo" (Bjornsson *et al.*, 2014), "rgeos" (Bivand and Rundel, 2014), "maptools" (Bivand and Lewin-Koh, 2014), and "maps" (Becker and Wilks, 2013).

Data from 2010 were excluded from the index due to insufficient survey coverage.

Results

Catch-rate models

Initially, three separate LGC models were fitted to subsets of the mackerel catch data. The first model was fitted to the data from IBTS Q4 surveys north of 44° that use comparable gears. The second model was fitted to the demersal trawl data from the survey along the north Spanish coast (Cantabrian Sea). This survey uses the smaller and incompatible BAKA trawl. The third model was a fit to IBTS Q1 data from the North Sea and west of Scotland. The parameter estimates and standard errors of each model are given in Supplementary Table S1, and average catch rates are mapped in Figures 2–4 and in Supplementary Figure S1. Juvenile mackerel have also been caught in the Faroese survey since 2007 and in the Icelandic surveys since 2006, but the catch rates were too low to allow for model fitting (Table 2, and maps in Supplementary Figures S2–S3).

Model performance was investigated by fitting an additional two models, restricted to data from areas common to the Q4 and Q1 surveys (55–60°N 4–10°W). The parameter estimates and standard errors for these runs are described in Supplementary Table S2. A comparison of the time-series from these fits show a statistically significant positive correlation ($p < 0.001$, $r^2 = 0.66$, Figure 5). The model was thus successful in extracting a common signal from the noise. The simplest explanation for this signal in catch rates is that it reflects mackerel population density. Furthermore, it indicates that the recruits are either relatively stationary from Q4 to Q1 or changes due to immigration are matched by those due to emigration. If there is any movement from Q4 to Q1, it is assumed that the direction of the movement follows the environmentally driven southwestward migration of the adults away from the cooling waters in the downstream, cold northwest end of the shelf and shelf edge current (Jansen *et al.*, 2012b). The correlation suggests that it is appropriate to consider the data from both Q4 and Q1 surveys simultaneously, and that recruits have not been double-counted due to the differences in timing between surveys. Data from Q4 and Q1 surveys should be directly combined because the comparison did not indicate a statistically significant difference in catchability (H_0: slope parameter not different from 1.0; $p = 0.134$).

Parameter estimates and standard errors from the model run including data from both Q4 and Q1 simultaneously are given in Table 3. The mackerel catch rates were found to be spatially correlated with a decorrelation distance (H) of 255 km. The spatial intercept surface explained approximately as much of the variance as the annual deviations from this intercept surface ($\sigma^2_{is} \approx \sigma^2_{ys}$). The nugget effect was estimated to be of relatively minor importance ($\sigma^2_N << \sigma^2_{ys}$). The spatial patterns of the cohorts were found to be significantly correlated from year to year with a temporal decorrelation period (T) of 0.8 years. The effect of this correlation was minor compared with the similarities modelled by the spatial intercept surface. Faster hauls were, as expected, found to increase the catch rates (Table 3). The effect of wingspread was not significant, while haul duration appeared to have a significant negative effect (Table 3).

Catchability

Analysis of acoustic data showed that mackerel schools directly within reach of the trawl were significantly larger than those in midwater (Figure 6, $p < 0.001$), i.e. the bigger schools were more demersal and accessible to the trawl than the smaller ones. Although catchability is a complex process affected by many factors, this observation suggests that a density-dependent transformation of catch rates should be considered when using these observations as proxies for mackerel abundance.

Comparison with ICES assessment

A recruitment time-series index was derived from the modelled catch rates (Q4 and Q1 combined). Additional indices were furthermore derived from cell-by-cell transformed catch rates to account for density-dependant catchability. The annual catch-rate indices were observed to vary substantially from year to year, demonstrating substantial interannual variation in cohort abundance (Figure 7),

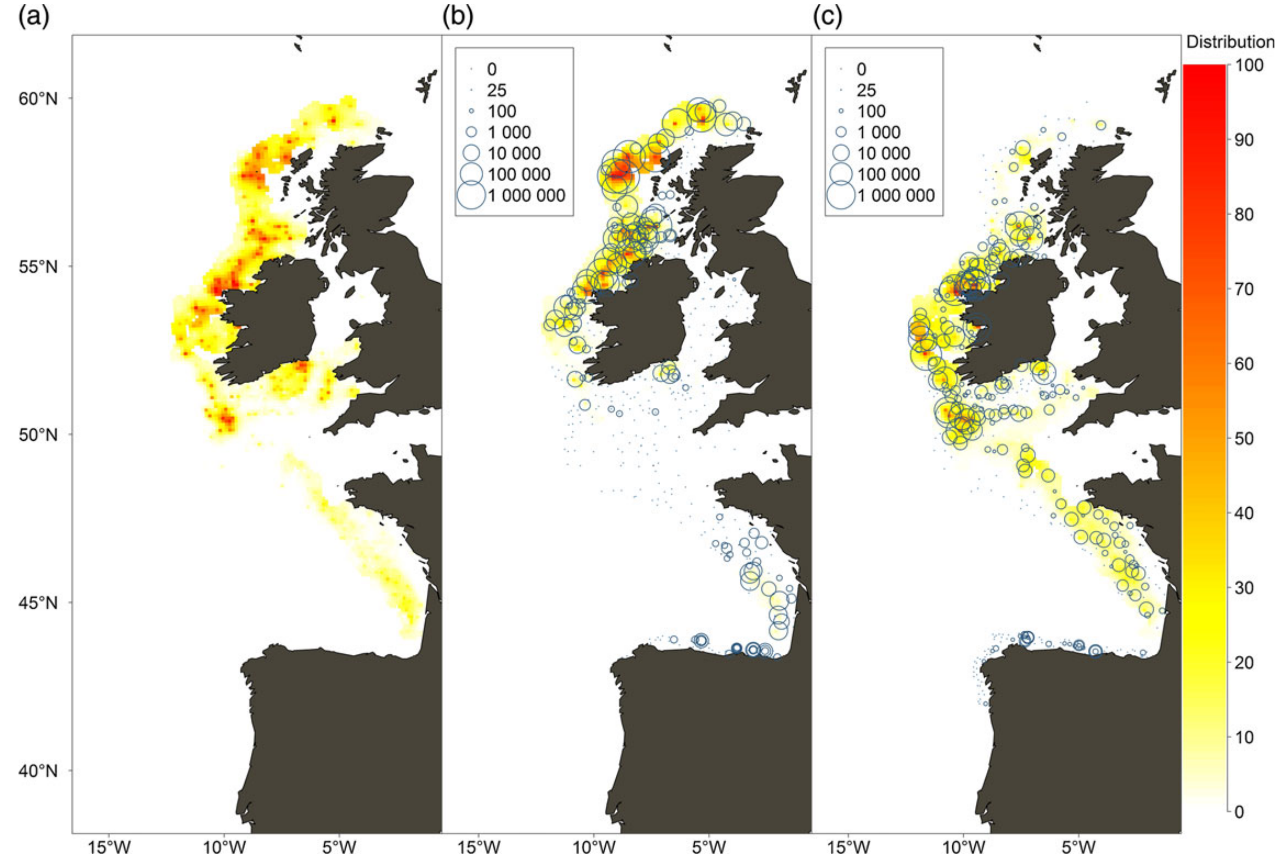

Figure 2. Distributions of catch rates of mackerel at approximately 3–9 months of age in the fourth-quarter demersal trawl surveys. (a) Average rates for 1998–2012 and the years with the highest catch rates in the time-series; (b) 2005; and (c) 2012.

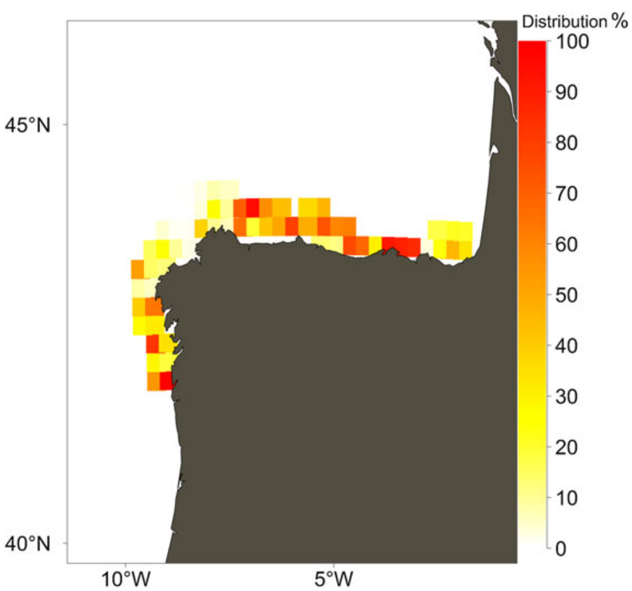

Figure 3. Modelled catch-rate distributions of mackerel at approximately 7–11 months of age in fourth-quarter demersal trawl surveys in Spanish waters. These catch rates are from trawling with a BAKA trawl and are, therefore, not comparable with the catch rates from the GOV trawl (all other figures).

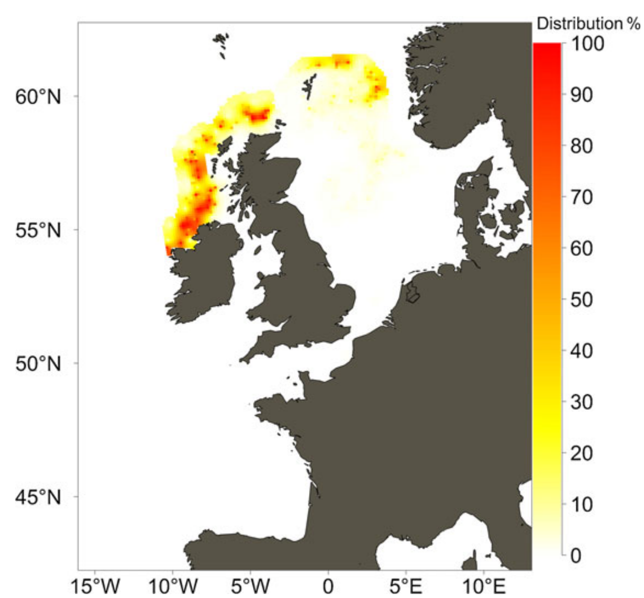

Figure 4. Modelled catch rates distributions of mackerel at approximately 8–11 months of age in first-quarter demersal trawl surveys.

Table 2. Comparative catch statistics for the bottom-trawl survey around the Faroe Islands, Iceland (south of 66°N), and the IBTS surveys.

Year	IBTS Q4 + Q1		Faroe Islands Q1		Iceland Q4		Iceland Q1	
	Mean no. nautical mile^{-2}	Presence (%)	Mean no. nautical mile^{-2}	Presence (%)	Mean no. nautical mile^{-2}	Presence (%)	Mean no. nautical mile^{-2}	Presence (%)
1998	3479	23	0.0	0	0	0	0	0
1999	5957	15	0.0	0	0	0	0	0
2000	3787	14	0.0	0	0	0	0	0
2001	997	17	0.0	0	0	0	0	0
2002	3650	25	0.0	0	0	0	0	0
2003	10 430	19	0.0	0	0	0	0	0
2004	6865	19	0.0	0	0	0	0	0
2005	32 413	25	0.0	0	0	0	0	0
2006	27 696	29	0.0	0	21	<1	0	0
2007	15 283	21	18.9	1	1	<1	0	0
2008	7833	20	0.0	0	0	0	0	0
2009	12 598	17	1.6	2	0	0	0	0
2010	10 474	33	0.4	1	65	<1	1	<1
2011	21 720	41	16.6	10	–	–	57	<1
2012	13 449	52	0.0	0	11	<1	0	0

Mean catch in numbers per swept area was calculated as a plain average over all hauls. Presence (%) denotes the fraction of hauls with one or more juvenile mackerel.

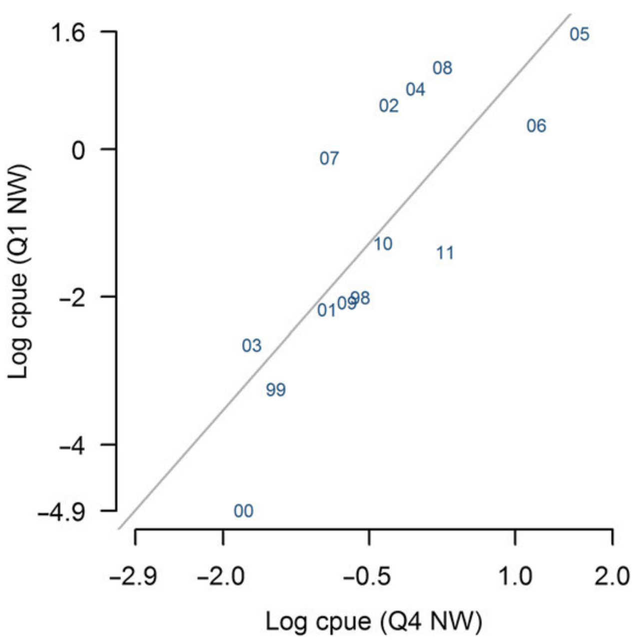

Figure 5. Cpue index of NEA mackerel in demersal trawl surveys. Fourth- and first-quarter surveys compared for the overlapping area (55–60°N 4–10°W). Numbers in the plot indicate the years.

consistent with the fishery-dependent data. The moderately transformed (square root and cubic root) indices were found to be most in accordance with the recruit abundance time-series estimated in the recent benchmarking assessment exercise for mackerel, providing further support for the hypothesis of density-dependent catchability (Table 4). The strongest correlation was found to be between the square root index and the base-case assessment (Assessment I, $p < 0.001$, $r^2 = 0.73$, Figure 7). Both of these time-series indicate three pulses of recruits, first in 2001–2002, then in 2004–2006, and finally in 2010–2012. The assessment indicates similar levels of all three pulses, while the estimate based on IBTS indicates that the 2001–2002 pulse was on a lower level.

None of the correlations between the indices and the final assessment (Assessment II) was statistically significant (Table 4).

Spatial variations in the catch rate

The estimated catch-rate distributions were square root transformed and mapped to show the general large-scale pattern (Figure 8). The highest densities were found in a band that runs from the southern Bay of Biscay, west of the British Isles, north of Scotland, and into the northern North Sea north of 59°N. The shelf around Ireland and Scotland in the northern North Sea appeared to be the most important nursery areas for the NEA mackerel (Figure 8). Juvenile mackerel were also caught in the Faroese survey since 2007 and in the Icelandic survey in 2004 and in 2011 (Table 2). The elongate band of high density that runs parallel with the shelf edge is, to some extent, segmented by two areas of relatively low density, namely west of the English Channel (49.5°N 8°W) and around the Fair Isle Channel (60°N 2.5°W; Figure 8). Juveniles were primarily caught at 20–200 m bottom depth (Figure 9).

Discussion

Based on consistent estimates from independent surveys that sample the same area in consecutive quarters, the LGC model described above is successful in extracting a signal from catch rates of juvenile mackerel that, most likely, reflects overall population abundance. This implies that the sampling noise is relatively low and/or is handled by the model. There are, however, a number of potential biases that may affect any proposed proxy for population abundance. Since several different vessel and gear combinations contribute to the IBTS dataset, any variation in gear set-up between individual surveys (areas) may affect catchability and result in a skewed distribution map. For example, the gear configuration used on the French survey (44–56.5°N) is similar to the standard GOV, except for the absence of a kite. However, by conducting a sensitivity analysis, this was found to be of minor influence on most years of the final index. This *post hoc* analysis considered indices calculated based on artificially inflated French catches (×2, ×4). These indices were strongly correlated with the final index (correlation coefficients of 0.89), demonstrating that the final index is fairly

Table 3. Model parameter estimates and standard errors.

Model	Symbol	Description	Unit	Estimate	s.e.	CV (%)
IBTS	T	Decorrelation time	Year	0.8	0.11	14
IBTS	H	Spatial decorrelation distance	Kilometre	255.2	33.38	13
IBTS	σ^2_{ys}	Spatial variance parameter (year-specific surfaces)	–	6.8	0.54	8
IBTS	σ^2_{is}	Spatial variance parameter (intercept surface)	–	5.0	0.54	11
IBTS	σ^2_N	Variance of the nugget effect	–	0.4	0.01	2
IBTS	$\log(GS)$	Log groundspeed	Nautical mile h^{-1}	1.6	0.14	9
IBTS	$\log(WS)$	Log wingspread	Nautical mile	−0.1	0.04	52
IBTS	$\log(D)$	Log haul duration	Hour	−1.2	0.37	31

All parameters were statistically significant ($p < 0.05$). Parameters with unit "–" are dimensionless.

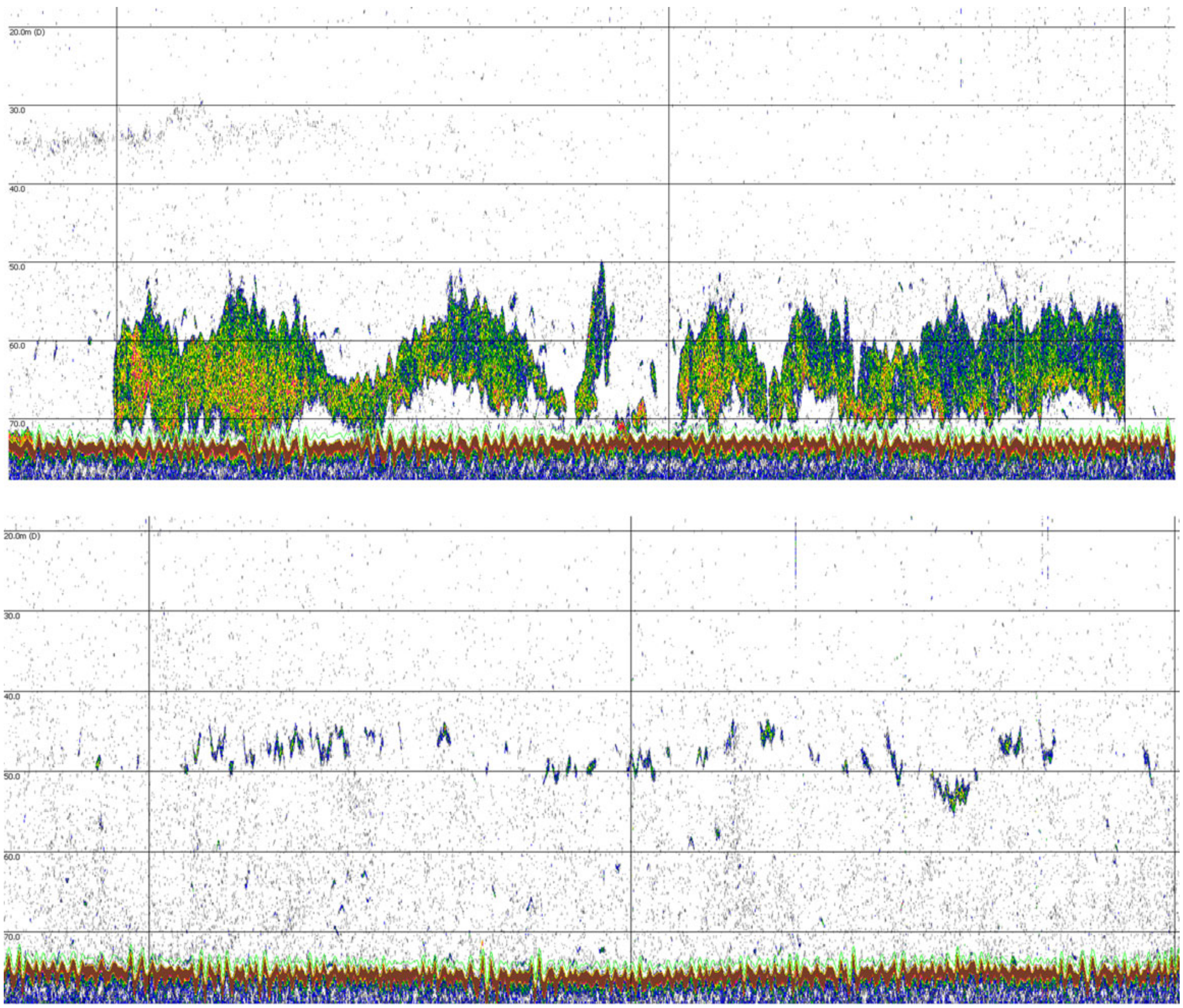

Figure 6. Echograms of typical large (top) and small (bottom) mackerel schools in the Celtic Sea area during October 2013. Horizontal lines represent 10-m depth bins and vertical lines indicate 1 nautical mile distance. Echograms were produced by applying a −70-dB post-processing threshold on 200 kHz backscatter recorded by Simrad EK 60.

robust to uncertainties about the catchability of the French trawl. Noteworthy deviations were mainly found in 2008, 2009, and 2012, indicating that the Bay of Biscay was of importance as a nursery area in these years (Supplementary Figure S4). An additional potential gear-related bias stems from size selectivity of the trawl, although this effect is considered to be negligible because the smaller fish (which are the subject of this study) would be fully selected, given the 10-mm mesh used in the codend of the GOV trawl. Catchability is proposed to be density-dependent, primarily because mackerel appear to aggregate close to the seabed in areas of increased density. Analytically, this effect can be incorporated in the model by a transformation of the catch-rate data. This

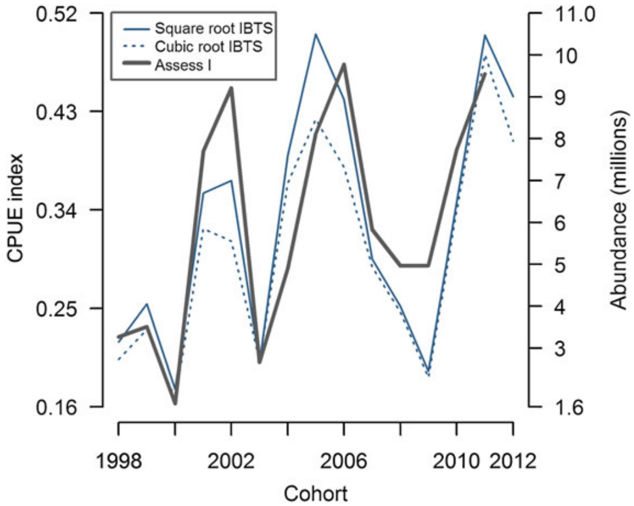

Figure 7. Comparison between IBTS recruitment index derived from square root transformed cpue (solid blue), cubic root transformed cpue (dashed blue), and the abundance of recruits estimated in the base-case assessment ("Assess I") in the ICES benchmark assessment workshop in February 2014 (solid grey).

Table 4. Comparison between of IBTS recruitment index with alternative transformations and the abundance of recruits estimated in the ICES assessment benchmarking workshop in 2014 (WKPELA).

	Assessment I		Assessment II	
Index	***p***	***r*²**	***p***	***r*²**
cpue (Q4 + Q1)	*0.140*	*0.17*	*0.285*	*0.09*
Square root cpue (Q4 + Q1)	$<$0.001	0.73	*0.167*	*0.15*
Cubic root cpue (Q4 + Q1)	$<$0.001	0.70	*0.279*	*0.10*
Log cpue (Q4 + Q1)	0.001	0.59	*0.545*	*0.03*

Assessment I is the pre-WKPELA assessment without the IBTS index and with the full time-series of IESSNS and tagging data. Assessment II is the ICES assessment based on the final WKPELA methods (ICES, 2014a). Italic values are statistically significant ($p < 0.05$).

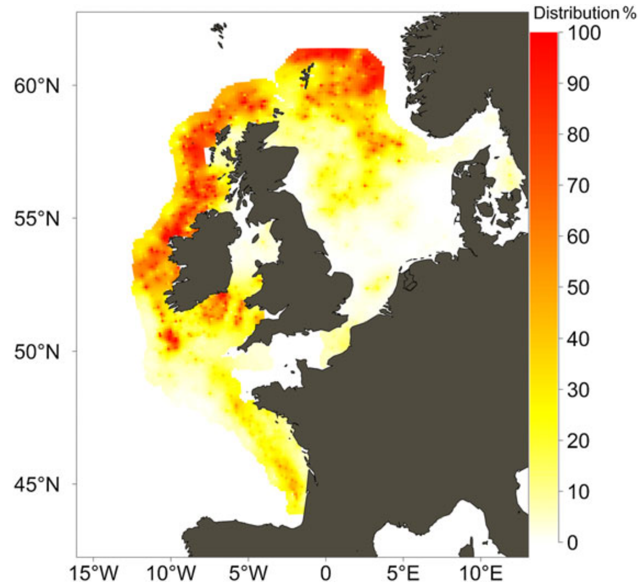

Figure 8. Distribution of juvenile mackerel during their first winter (October – March) proxied by modelled square root transformed catch rates in demersal trawl surveys.

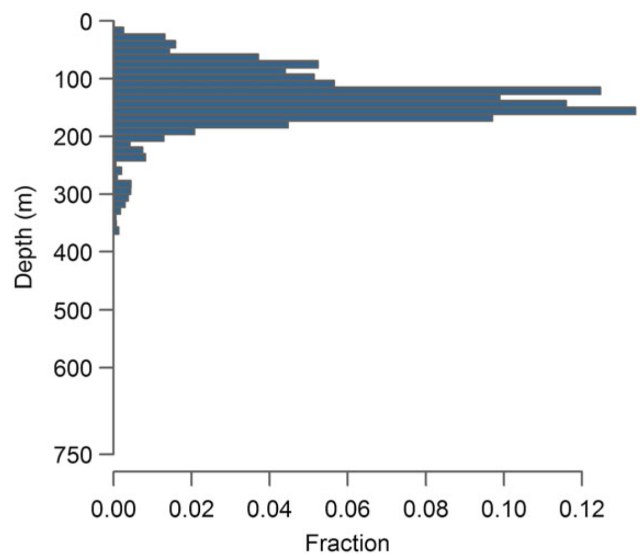

Figure 9. Depth distribution of juvenile mackerel during their first winter (October – March) proxied by modelled square root transformed catch rates in demersal trawl surveys.

tendency towards demersal behaviour by juvenile mackerel in the cold months (Figure 6) permits the catch rates derived from a bottom-trawl survey to be applicable to an otherwise pelagic species. Presence in the demersal zone, within reach of the bottom trawl, is further facilitated by a diving avoidance response to the approaching trawling vessel (Misund and Aglen, 1992; Slotte *et al.*, 2007). Juvenile indices have also been shown to be noisy, but informative in stock assessments of other pelagic stocks such as herring (ICES, 2013c).

Surveying a fish population that is widely distributed over large parts of the North Atlantic is a significant challenge. The realized coverage is ultimately a trade-off between the scientific aim to cover the distribution area in its entirety and logistical and economic realities. The combined surveys of the IBTS do not cover the entire distribution area for mackerel juveniles in their first winter, so the utility of the time-series depends heavily on the relative importance of the unsampled nursery areas. Conceptually, these areas can be subdivided into three types: the edges of the sampled areas, relatively small unsampled areas within the overall survey area, and large unsampled areas outside the survey areas. The surveys covered the shelf and upper shelf slope. This covered the shallow edge of the distribution well (Figures 1 and 9). Mackerel were, in most years, not found at the deepest stations. However, zero line was not reached in all years. Mackerel farther down the slope could, therefore, have been missed by the survey. Smaller areas within the main survey areas, such as the rocky unfishable seabed southwest of Hebrides and north of Orkney, are included in the spatial grid used by the model. Estimation of the cpue in these areas, as for all other unsampled cells within and along the edge of the survey area, was based on the spatio-temporal correlation parameters. This approach is efficient for interpolating, but has no merit in large unsampled areas outside the study area. Potential nursery areas include the spawning areas and the areas where the combined effect of advection and migration can bring mackerel from spawning in January–July to the time of the surveys (October–March). Over this time-span, mackerel grow from the larval stage (where movement is practically restricted to the vertical dimension) to a length of approximately 15–23 cm. Although mackerel have excellent swimming capabilities at this stage, information from tagging indicates that they do not migrate any significant distance (Uriarte *et al.*, 2001). The area of concern is, therefore, limited to the spawning area and areas immediately adjacent (downstream). Both the main spawning area and the area downstream (for several hundred kilometres) are covered by the surveys. Furthermore, catch rates around the Faroe Islands and Iceland were low compared with those on the European shelf, and the highest catch rates were consistently within (i.e. not at the boundaries) of the study area (Figures 2a and 4). It is, therefore, reasonable to assume that the combined surveys used in this analysis covered the most important nursery areas. However, although recruitment outside the study area may be currently of limited importance, the suggested trend in the expansion of the spawning area should be followed carefully. If significant proportions of the recruits appear outside the survey coverage, then the index will not be useful before the coverage is expanded accordingly.

Areas currently outside the IBTS coverage that merit further exploration include the oceanic areas north and west of the British Isles (including Rockall and Hatton banks), where spawning has been observed since the 2010 egg survey. The Norwegian shelf may also be of some importance. No comparable data are available from the latter area, but it is fair to assume that juveniles are present, given that relatively high concentrations close to the northeast edge of the IBTS survey are reported here and because juveniles have been observed farther north in demersal and pelagic trawl surveys in August–September in the western Barents Sea. Observations of mackerel ranging in size from 20 to 89 mm have been recorded as far north 76.5°N and east to 40.5°E (Supplementary Figure S5). A total of 827 juvenile mackerel were caught in 16 233 hauls between 1980 and 2013, so the catch rates in this area are very low. Mackerel were caught in every decade, but not in all years. The core of warm water close to the shelf break in the northeast extension of the North Atlantic Current, namely the Norwegian Current, would be a relevant area to explore based on the observations reported here that seem to follow the affinity of adult mackerel for warm water (Jansen *et al.*, 2012b).

The main nursery area in winter, as suggested by the model fit (Figure 8), resembles the distribution of the adults in winter. Adult mackerel migrate south along the continental shelf edge from mid-November to early March. The path of this migration coincides with the location of the relatively warm shelf edge current. Variations in the timing of the adult migration are significantly correlated with temperature fluctuations within the warm current (Jansen *et al.*, 2012b). If it is the case that juvenile mackerel respond to temperature variation in a similar way, then the fraction of the cohort that is northeast (outside) of the IBTS survey area will vary from year to year, reducing the signal-to-noise ratio of any recruit index derived from survey data.

ICES currently assesses mackerel in the North Atlantic as a single stock traditionally considered to consist of three spawning components: southern, western, and North Sea. This simplistic population model has recently been challenged by results, indicating structures within the spawning components (Jansen *et al.*, 2013) and substantial straying among the spawning components (Jansen and Gislason, 2013). A more complex population model is, therefore, needed to represent actual details and dynamics. The elongate band of high density that runs parallel with the shelf edge was, to some extent, segmented by two areas of relatively low density, namely west of the English Channel (49.5°N 8°W) and around the Fair Isle Channel (60°N 2.5°W) (Figure 8). The Fair Isle Channel is also known to form a discontinuity in the spawning area and has been regarded as the border between the western and North Sea spawning components (Jansen and Gislason, 2013). However, the area west of the English Channel (49.5°N) is in the middle of the spawning area for the western component, and a study that suggested spatial segregation within the western area did not indicate an abrupt shift around 49.5°N (Jansen *et al.*, 2013). The new maps of nursery areas presented here may, if considered year by year, contribute to future analyses of the unresolved issue of the population structure of mackerel in the NEA.

When benchmarked against an alternative raising procedure for the recorded catches (based on swept area), the LGC model performed appreciably better. This was seen on the stronger correlation ($p = 0.001$, $r^2 = 0.66$ compared with $p = 0.008$, $r^2 = 0.48$) between the index in Q1 and Q4 in the area of overlap. This is the first benchmark of the commonly used procedure against the LGC model approach for generating cpue-based abundance indices for stock assessment.

The recruitment time-series available from this analysis has been used as an index for the mackerel stock assessment since 2014 (ICES, 2014a). Its inclusion, however, had a limited influence on the assessment output primarily because the commercial catch data were not in agreement with the IBTS survey time-series (Assessment II, Table 4). This was in contrast to the strong correlation with the base-case assessment (Assessment I) that included all available input data (except the IBTS series), i.e. where all tagging data and the IESSNS survey contributed to the estimation of the last 6–8 cohorts (Table 4). The current level of uncertainty in the assessment outputs is too high to conclude which of the inputs provides the most appropriate recruit estimates. This may be resolved over time as the various new fishery-independent time-series are extended.

Conclusions

A strong correlation between the independently sampled and modelled juvenile mackerel catch rates in Q1 and Q4 suggests that the LCG process model was successful in extracting a population abundance signal from the data. The model's performance was appreciably better than a raising algorithm based on swept-area estimates.

The recruitment time-series available from this study has been incorporated in the latest mackerel assessment model (ICES, 2014a), although the recruitment index was more strongly correlated with an alternative assessment to the final configuration, questioning whether the removal of some input data actually improved the estimation of the relative cohort sizes. The level of uncertainty in the assessment is currently too great to draw conclusions on the historical performance of the index.

A hypothesis of positive density-dependant catchability was suggested. This hypothesis was supported by an analysis of acoustic observations and through the application of a square root transformation to the raw catch-rate data that resulted in an improved index.

The most important nursery areas for the NEA mackerel appeared to be around Ireland, north and west of Scotland, in the northern North Sea north of 59°N, and, to some extent, also in the Bay of Biscay. It is argued that the surveys that were included in the analysis covered the most important nursery areas. Comparative surveys or exploratory sampling should be conducted in oceanic spawning areas such as Rockall Bank, Hatton Bank, and the Norwegian shelf, because these areas may become increasingly important. Furthermore, gear standardization should be achieved between all areas.

The novel estimate of spatio-temporal recruit distribution can facilitate novel studies, such as density-dependant growth (Jansen and Burns, in press), environmental characterization of the nursery habitat, as well as one of the most important aspects of the biology of an exploited species: drivers of recruitment variability.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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